Diet Differentiation in Three Species of Juvenile Pacific Salmon (*Oncorhynchus* spp.) in Estuarine Tidal Channels and Laboratory Experiments

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2007

Canadian Technical Report of Fisheries and Aquatic Sciences No. 2758

Fisheries and Oceans Pêches et Océans

Canada

Canadian Technical Report of Fisheries and Aquatic Sciences

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2008-01113/

Canadian Technical Report of
Fisheries and Aquatic Sciences 2758

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DIET DIFFERENTIATION IN THREE SPECIES OF JUVENILE PACIFIC SALMON (*ONCORHYNCHUS* SPP.) IN ESTUARINE TIDAL CHANNELS AND LABORATORY EXPERIMENTS

by

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Cat. No. Fs 97-6/2758E ISSN 0706-6457

Correct citation for this publication:

Magnhagen, C., Northcote, T.G., and Gregory, R.S. 2007. Diet differentiation in three species of juvenile Pacific salmon (*Oncorhynchus* spp.) in estuarine tidal channels and laboratory experiments. Can. Tech. Rep. Fish. Aquat. Sci. 2758: vi + 20 p.

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ABSTRACT

Magnhagen, C., Northcote, T.G., and Gregory, R.S. 2007. Diet differentiation in three species of juvenile Pacific salmon (*Oncorhynchus* spp.) in estuarine tidal channels and laboratory experiments. Can. Tech. Rep. Fish. Aquat. Sci. 2758: vi + 20 p.

The aim of this study was to determine if juveniles of Pacific salmon species, that occupy Fraser River estuary tidal channels, utilize the same resources and if there was an effect of species co-occurrence on diet. Enclosure experiments were performed to study diet of juvenile pink, *Oncorhynchus gorbuscha*, chum, *O. keta*, and chinook salmon, *O. tshawytscha*, salmon, when species were held alone and together. Diet overlap between the species was high in 1986, comparing all three species, but in 1989, when only chum and chinook were present in the estuary, the overlap was lower. Differences in diet could be recognized in both years. Pink fed mainly on harpacticoid copepods. This was also the most common prey item for the other species, but chum also ate other benthic species and chinook fed more on adult insects than did the others. An aquarium experiment studying prey utilization in chum and chinook, separately and together, gave similar results as the field enclosures, with chinook taking more surface prey than did chum when kept together and chum eating more small *Daphnia*. This study shows that these three salmonids differ in their use of food resources in tidal channels, and that these species potentially can influence the diet of each other when co-existing.

RESUMÉ

Magnhagen, C., Northcote, T.G., and Gregory, R.S. 2007. Diet differentiation in three species of juvenile Pacific salmon (*Oncorhynchus* spp.) in estuarine tidal channels and laboratory experiments. Can. Tech. Rep. Fish. Aquat. Sci. 2758: vi + 20 pp.

L'objectif de cette étude était de déterminer si les juvéniles des espèces de saumon du Pacifique présents dans les chenaux de marée de l'estuaire du Fraser utilisent tous les mêmes ressources et si la présence simultanée d'espèces a une incidence sur les régimes alimentaires. Nous avons réalisé des expériences en enclos afin d'étudier le régime alimentaire des juvéniles du saumon rose (Oncorhynchus gorbuscha), du saumon kéta (O. keta) et du saumon quinnat (O. tshawytscha) lorsque les trois espèces sont isolées et lorsqu'elles se côtoient. Le chevauchement alimentaire entre les espèces était élevé en 1986, si l'on compare les trois espèces, mais il était moins important en 1989, année où seuls le saumon kéta et le saumon quinnat étaient présents dans l'estuaire. Des différences sur le plan du régime alimentaire ont été observées les deux années. Le saumon rose a consommé surtout des harpacticoïdes, et ceux-ci étaient également la proie la plus fréquente des autres espèces de saumon. Le saumon kéta s'est également nourri d'autres espèces benthiques, tandis que le saumon quinnat a consommé davantage d'insectes adultes que les autres espèces.

Une expérience en aquarium axée sur le choix de proies par les saumons kéta et quinnat a donné des résultats semblables aux expériences en enclos : le saumon quinnat consomme davantage de proies de surface que le saumon kéta lorsque les deux espèces se côtoient, et le saumon kéta consomme davantage de daphnies. Cette étude montre que ces trois espèces de salmonidés utilisent les ressources alimentaires des chenaux de marée de façon différente et que chaque espèce peut avoir une incidence sur le régime alimentaire des deux autres lorsqu'elles partagent le même milieu.

INTRODUCTION

The Fraser River in British Columbia, Canada, is the greatest producer of salmonid fishes in the world (Northcote and Larkin 1989). Hundreds of millions of juvenile Pacific salmon annually migrate downstream through its estuary (Northcote 1974), and at least three of these species (pink, *Oncorhynchus gorbuscha*; chum, *O. keta*, and chinook salmon, *O. tshawytscha*) spend from one to several weeks feeding in tidal channels of its lower estuary (Levy and Northcote 1982). Trophic interactions among juvenile Pacific salmon in coastal waters and outer estuarine habitats have been the subject of many studies in recent decades (Healey 1982a, 1991; Levings 1982, 1985; Miller and Simenstad 1997). However, inner estuarine tidal channel habitats also may be heavily by young salmon for feeding (Levy et al. 1979; Levy and Northcote 1981, 1982). Hood (2002) suggested that highest concentrations of feeding fish occur in either the upper reaches of small estuarine tidal channels or in the small distal portions of large ones. With multiple species confined to restricted areas, there is potential for interspecific competition for food and resultant effects on growth and survival, as found in pink salmon (Beacham 1993). Feeding interactions among potential competitors among young-of-the-year fishes have been studied in field enclosures (McGreer et al. 1983, Richardson and Threlkeld 1993, Abrahams 1996), and in fish tanks, for example, juvenile Atlantic salmon (*Salmo salar*) and steelhead (*O. mykiss*) (Volpe et al. 2001), small Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) (Jansen et al. 2002), and subadult percids (Savino and Kolar 1996).

In a companion study (Northcote et al. 2007), we examined the use of space and prey types by three species of young-of-the-year Pacific salmon, which temporarily cohabit the inner tidal marsh channels of the lower Fraser River estuary. In that study, we found that these species partially segregate spatially into microhabitats, and by diet choice. In the present study, we present results of a series of field experiments performed in the Fraser river tidal channels to examine the prey utilization of these species. Fish were held in enclosures fixed to the bottom of these tidal channels as: 1) single species, 2) species pairs, and 3) species triads. We conducted laboratory studies to test for diet segregation between juvenile chum and chinook salmon, the two species which in the field seemed to have the highest overlap in resource use (Northcote et al. 2007). The aim of both the field and laboratory studies was to determine the degree of dietary overlap among the three species while they were present in tidal channels and the effect of species co-occurrence on diet.

METHODS

FIELD ENCLOSURE EXPERIMENTS

Prey use by juvenile salmon in tidal marsh channels of the lower Fraser River estuary was examined experimentally, using cylinders (H = 2.5 m; D = 0.5 m) open at their top and bottom (Fig. 1). Cylinders were made from perforated

aluminium screening with hexagonal-shaped openings 4.6 mm in maximum width. Openings permitted invertebrate prey passage into and out of the cylinders while retaining salmon juveniles. Cylinders were pushed 5 cm into the soft mud bottom near the channel centre at low tide, the evening before experiments started, and were held in vertical position by metal rods during overnight channel filling and next-day dewatering by tidal change. Tidal channel D4 (Levy and Northcote 1981, Fig. 4) was used for enclosure experiments with different species combinations in 1986 and 1989. Three species of young salmon – pink, chum, and chinook – were available in 1986. Mean fork lengths (± S.D.) were 34.0 ± 1.5 (n=47), 39.0 ±1.9 (n=66), and 41.0 ± 3.0 (n=41) mm, respectively, with no significant difference between test dates. There was a significant difference in size between the three species ($F_{2,133}$ = 121.6, p<0.001). Only chum and chinook were used in 1989 as pink young are virtually absent from the river on odd numbered years (Northcote and Larkin 1989). Mean fork lengths (± S.D.) were 37.8 ± 1.7 mm (n=125) for chum in April and May 1989, with no size difference between months (t=0.58, p=0.56, df = 123). Chinook were larger than chum (t = 5.10, df =136, p < 0.001), and were also larger in April compared to May (39.8 ± 2.2 (n=80) and 42.3 ± 4.0 (n=111), respectively; t=6.2, p < 0.001), df =189).

Young-of-the-year salmon were captured using an intertidal trap net (Levy and Northcote 1982) the day before experiments started. Juveniles used in experiments were kept in the channel for 18 hours in 55 cm high and 45 cm diameter covered plastic containers with 100 μm screened openings just below the water level and at mid-depth for through flow. The containers, therefore, were filled with 100μm filtered tidal channel water. Over the 18 h holding period the guts of juveniles were largely evacuated, as found when we compared fish preserved immediately after capture with fish that had spent 18 hours in the containers Number of prey found in the stomachs decreased from an average of more than 100 to a maximum of 5-6.

The young salmon were introduced to enclosure cylinders near dawn at about the maximum water level in the channel. After the water level dropped to 10 cm above the mud bottom (about 3 h) the experiment was terminated, the young salmon removed, killed in anaesthetic (MS 222; Tricaine Methanesulfonate), and preserved in 5 % formalin for later analyses. Analyses included determination of fork length, weight, and stomach contents. Ingested prey were categorized into major taxa using dissecting microscopes (10–50x magnification). Total counts were made for each prey taxon and volumes estimated by liquid displacement in a volumetric tube. Stomach fullness index was estimated on a scale between 0 and 5–0 being empty and 5 totally full.

There are many ways to express diet composition in fish and these have been reviewed several times (Hyslop 1980; Macdonald and Green 1983; Hartman and Brandt 1995; Cortés 1997; Liao et al. 2001). We quantified diet composition as percentage of prey types by numbers and volumes for each fish, as well as

percentage occurrence of different prey types. Diet composition was calculated only using fish with food in their stomachs.

Diet overlap between species was calculated by using Schoener's index (Schoener 1969). Indices were calculated both on percentage of volume of different prey types in each stomach and percentage of numbers, since these two indices differ substantially if there are big size differences between different prey types. The percentage volume of a prey gave its relative importance to total energy intake, while percentage of numbers demonstrated relative foraging activity directed toward specific prey taxa. An overlap index >60% was considered significant (see also Hirst and DeVries 1994; Aku and Tonn 1999; and Degerman et al. 2000).

LABORATORY EXPERIMENTS

Young chum and chinook salmon (37.5 ± 5.9, 42.9 ± 3.6 mm mean fork length ± SD, respectively) were collected by beach seine in May to early June, 1985, in the field study tidal channels of the lower Fraser River estuary and transported to the laboratory in 100 L plastic containers filled with tidal channel water. Fish were kept in the laboratory in 200 L holding tanks and fed daily with dry commercial fish food.

Experiments were conducted in 30 L aquaria filled with dechlorinated water (10-12°C) to a depth of 20 cm and with a 3 mm layer of tidal channel sediment on the bottom. Half of the replicate runs were carried out in clear water, in order to make behavioural observations possible. Turbid water (approximating that in the tidal channels), obtained by appropriate addition of fine tidal channel sediment and remaining in suspension over the 2 h experimental period, was used.

Three types of invertebrate prey were chosen to represent largely benthic (chironomid larvae), midwater (*Daphnia pulex*), and surface dwelling (*Drosophila melanogaster*) forms. Fifty chironomid larvae (tidal channel source) about 10 mm long were placed on the bottom of each aquarium about one hour before the experiments started; they immediately burrowed into the sediment. One hundred large *D. pulex* (2-3 mm) were placed into small plastic containers 2 d before an experiment where they reproduced providing several hundred small (0.2-0.3 mm) offspring. Daphnids from one container were added to each aquarium just before the experiment started. Twenty *D. melanogaster* (about 3 mm in length) were tranquilized by placement in a freezer for a few seconds and then dropped onto the water surface of each aquarium where they remained alive.

Experimental trials were run with fish starved for 24 h (four chum, four chinook, or two individuals of each species per aquarium) for 2 h during daylight. Fish were then killed in anaesthetic (MS 222) after 2 h and preserved in 70% alcohol. Stomach contents were excised and the number and size class (daphnids only) of each prey type were noted. The mean number of prey ingested from each category was calculated, for statistical purposes, for each replicate aquarium, in

order to avoid pseudoreplication. In mixed-species aquaria, mean values for each species were calculated. Fish with empty stomachs were omitted from calculations; means were calculated by dividing total number of prey eaten by number of actively feeding fish. The experiments were repeated eight times for individual species trials, and 16 times for two-species trials.

In the clear water aquaria, one glass wall was marked with horizontal lines at 5 cm intervals. During the feeding experiments, depth of each fish was noted every 30 min (four times during each experiment). Number of fish found at different depths during the four observations was pooled for each aquarium and divided by four to obtain the mean number of fish occurring at the separate depth levels for each replicate.

RESULTS

FIELD ENCLOSURE EXPERIMENTS

Nine prey taxa were commonly found in the stomachs of fish after the termination of the 3-h enclosure trials. Different prey use different microhabitats and we defined them as benthic (*Corophium* sp., *Anisogammarus* sp., harpacticoid copepods, insect larvae, ostracods), midwater (*Neomysis* sp., cyclopoid copepods, insect pupae) and surface prey (insect adults). Insect prey were divided into the above three types according to their development stages (larvae, pupae, adults) that mainly occupy the three different microhabitats. Insect groups consisted mainly of chironomids, in all three stages. Some prey types found only in a few cases, such as *Nereis* sp., *Daphnia* sp., and Collembola, were not included in the presentation of diet compositions.

In 1986, most fish from the enclosures had food in their stomachs, while, in 1989, the number of empty stomachs was higher, and in many enclosures exceeded 50% (Table 1).

1986

Pink salmon fed mainly on harpacticoids, both when alone in the enclosures and in the two or three species combinations (Fig. 2 and 3). The only other prey found in pink stomachs were *Anisogammarus* and ostracods, both benthic organisms. Like pink, chum salmon also ate mainly harpacticoids, but included all the other benthic taxa in their diet as well. They occasionally had adult insects in their stomachs, indicating that they also fed from the surface (Fig. 2 and 3). Chinook included prey from all microhabitats in their diet, but harpacticoids were still the most common prey item (Fig. 3).

Chinook seemingly had a broader diet than chum and pink, on the basis of prey types consumed (Fig. 3). Overlap in diet, however, calculated with percentage volume and percentage composition by numbers, was very high for all species and dates, both when the species were alone and in different species combinations (Table 2). In one case only, when chinook and pink were together,

was the overlap non- significant (i.e. <60%). The high overlap indices were due to a very dominant role of harpacticoids as prey for young salmon in general. There was no difference in fullness index between species (Kruskal-Wallis $H_{2,256} = 0.88$, $p = 0.64$).

1989

Chum and chinook both used the same eight prey types in the enclosures (Fig. 4), however, overlap in diet, calculated on percent volume, was significant only when species were kept alone (Table 2). The overlap index was also always lower when the species were together in the enclosure compared to when species were alone. Harpacticoids were always found in higher volumes in chum than in chinook; in contrast, chinook had higher volumes of adult insects in their stomachs (Fig. 4). Overlap index, calculated on percent number of different prey types, had highly variable results (Table 3). Harpacticoid copepods influenced these indices to a large degree, as number of harpacticoid copepods eaten was higher than other prey, even when the volume was lower. The prey of different categories were used in different frequencies in the two species (Table 3); chinook consumed more adult insects and *Corophium* on average than chum, while chum ate more harpacticoids. Fullness index (including empty stomachs) differed between the species (Kruskal-Wallis $H_{1,273} = 5.96$, $p = 0.015$), with chum having a higher average fullness than chinook (Table 1).

AQUARIUM EXPERIMENTS

There was no difference in prey utilization between clear water and turbid water aquaria in either fish species (Two-way MANOVA; Wilks' lambda (df: 3, 42) = 0.50, $p<0.001$ (species); 0.96, $p = 0.65$ (water); 0.95, $p = 0.51$ (species x water); therefore, we pooled results from clear and turbid water treatments in further analyses.

Prey utilization by chum and chinook did not differ when alone, but both species changed their diet when together in aquarium trials (Two-way MANOVA; Wilks' lambda (df: 3, 42) = 0.56, $p<0.001$ (species); 0.90, $p = 0.21$ (treatment); 0.74, $p = 0.005$ (species x treatment; Fig. 5). There was no difference in the mean number of *Drosophila* eaten when alone (Tukey post-hoc test; $p = 0.71$). Chinook ate significantly more *Drosophila* than did chum when together (Tukey post-hoc test; $p<0.001$). Chum always ate more small *Daphnia* than did chinook (Tukey post-hoc test; $p = 0.001$) when together, but not when alone (Tukey post-hoc test; $p = 0.93$), and there was a tendency for chum to increase number of small *Daphnia* eaten in presence of chinook (Tukey post-hoc test; $p = 0.087$). There were no differences in mean number of large *Daphnia* ingested between the species, either when alone or together (Tukey post-hoc test; $p = 0.86$-1.00). Chironomid larvae were found only eight times in chinook and two times in chum, which suggested some difference between species, but numbers were too low to test statistically.

Depth distribution differed between the two species (Fig. 6). Chinook were evenly distributed in the water column, both when alone (Median test; df = 3; $\chi^2 = 6.86$, $p = 0.077$) and when together with chum ($\chi^2=4.85$, $p=0.18$). More chum occurred in the lower half of aquaria, both when alone ($\chi^2 = 10.0$, $p = 0.019$), and when together with chinook ($\chi^2 = 12.8$, $p = 0.005$).

DISCUSSION

We found clear differences in food intake between species, especially in number of prey types taken in field experiments. Pink salmon were only available for 1986 experiments and fed almost exclusively on harpacticoid copepods, and seldom on other benthic taxa. Chum had a broader diet, but ate mainly benthic species. Chinook diet was similar to that of chum, but they also fed on mid-water and surface prey. These results correspond with our field study from the same area in the Fraser River estuary (Northcote et al. 2007). However, there were differences between studies regarding diet overlap between the species. The field study showed a low overlap between pink and the other species, however, overlap indices (Schoener 1969) were significant among all species in 1986 enclosure experiments. Microhabitat utilization differed between species in the field study, with chum and chinook occupying channel edges to a greater extent than pink, which mainly occupied the centre of the channel. Higher availability of adult insects at the edge of the channel (e.g. insects falling from the overhanging shoreline vegetation) may explain the higher ingestion of surface prey in chum and chinook, in contrast with pink. All fish were forced to occupy the same habitat within the enclosures in our field experiments and the high utilization of harpacticoids by all species probably resulted from the availability of that prey type. Other field studies also show spatial segregation among co-occurring juvenile salmon in estuaries (Murphy et al. 1988 and Dauble et al. 1989) and in streams (reviewed by Bremset and Heggenes 2001), and use of available prey types in these microhabitats (Macdonald et al. 1987 and Shreffler et al. 1992). Potential competition between pink and chum fry from the Fraser estuary has previously been found in experiments, where both species experienced decreased growth rate with a higher relative abundance of chum (Beacham 1993). In our study, we did not know if the food resources were limiting in the estuary or in enclosures, and therefore cannot conclude that differences in use of prey types and space were solely related to interspecific competition. Occupation of different microhabitats would, however, reduce risk for interspecific competition.

Diet overlap between chum and chinook was not significant in 1989, and was generally lower in enclosures where species were together compared to when alone. Chum fed primarily on benthic prey in 1989 while chinook ate more surface prey than did chum. Chinook ate more from the water surface than other species, therefore variation in abundance of insect adults might explain a variation in diet overlap. However, no data were collected to address this issue.

Results from aquarium experiments corresponded well with results from enclosures in 1989. Chinook in aquaria took more surface prey (*Drosophila*) than did chum when together, similar to enclosure results. Chum also ate more of the smallest prey (small *Daphnia*) than did chinook, just as they ate more of the smallest prey (harpacticoids) in the enclosures. Food availability in aquaria was limited, especially *Drosophila*, that were depleted in most cases. Chinook consumed most of the *Drosophila* when together with chum and this could depend on differences in vertical distribution within aquaria, even though these were only 20 cm deep. Chum mainly occupied lower parts of the aquaria, while chinook were more dispersed in the water column and would be more often close to prey on the water surface. Fish distribution in the enclosures is unknown, however, higher ingestion of adult insects by chinook suggest they spent more time near the water surface than did chum. Chinook were found in higher densities near the surface compared with chum in our field study (Northcote et al. 2007).

Design of enclosure experiments in 1986 was not optimal, as several species combinations could not be replicated due to fish availability. This deficiency could have caused a problem, had we found substantive differences in diets between enclosures, since confounding treatment and enclosure effects could have explained results. In one case only, when chinook co-occurred with pink, was there a decrease in utilization rate of harpacticoid copepods by chinook. Overlap indices were otherwise high, both when comparing enclosures with species separate and when together, suggesting that species composition did not influence diet during 1986 field experiments.

Size differed among the three species. Chinook was the largest species, and pink the smallest. Larger salmon are generally able to feed on larger prey; however, diet reflects both preference and prey availability (Healey 1991). Chinook ingested more larger prey types than other salmon species, but still included harpacticoids in their diet. The fact that chinook had a broader diet than other species suggested that this species could have a feeding 'refuge' if overall fish density were high.

In conclusion, we have shown that diet composition of pink, chum and chinook salmon are similar, while there is potential for diet segregation, since chinook eat more larger and more surface prey than the other species. Juvenile salmon spend a limited time in the Fraser river tidal channels, however, growth rate during this time may be crucial for future survival. For example, (Healey 1982b) found that mortality just after migration into marine habitats was size-selective in chum. The same pattern has also been found in other Pacific salmon reviewed in (Sogard 1997). It is therefore likely that flexibility in diet, adjusting to density of juvenile salmon, as well as to prey availability in tidal channels, is important for maximizing growth rates and survival probabilities of migrating juvenile salmon.

ACKNOWLEDGMENTS

Financial support was provided by a Natural Sciences and Engineering Council (NSERC) research grant to TGN, a NSERC Postgraduate Scholarship to RSG and a Swedish Natural Science Research Board (NFR) Postdoctoral Fellowship to CM. The Swedish Foundation for International Cooperation in Research and Higher Education (STINT) made the finalization of the manuscript possible. Assistance in the field and laboratory was provided by numerous students at the University of British Columbia; including: D. Atagi, I. Leroy, E. Power, R. Schiffer, L. Sennewald and T. Suzuki. Comments on an earlier draft by B. Laurel and D. Scruton, improved the final manuscript.

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Table 1. Number of fish with food in their stomachs versus total number of fish in each enclosure, and mean (±SD) stomach fullness (F) (ranked on a scale 0-5, with 0 empty and 5 full) in (a) 1986 and (b) 1989. Letters before the data denote the different replicates.

	25 April		**9 –10 May**	
(a) 1986	w. food/total	Fullness	w. food/total	Fullness
alone				
Pink	22/24	2.71 ± 1.73	22/23	1.39 ± 0.58
Chum	23/23	3.26 ± 1.21	21/23	2.26 ± 1.05
Chinook			16/24	1.92 ± 1.56
together				
Pink	10/11	2.36 ± 1.36	12/12	1.67 ± 0.39
Chum	11/12	2.17 ± 1.34	10/12	1.25 ± 0.87
Pink			12/12	2.50 ± 0.52
Chinook			8/12	2.42 ± 1.97
Pink			a 9/9	2.67 ± 0.50
			b 5/6	1.67 ± 0.75
Chum			a 3/6	0.67 ± 0.82
			b 7/7	3.71 ± 1.78
Chinook			a 6/9	1.56 ± 1.59
			b 8/10	2.40 ± 1.71
	20-22 April		**8-10 May**	
(b) 1989	w. food/total	Fullness	w. food/total	Fullness
alone				
Chum	a 10/20	0.80 ± 1.00	18/20	1.80 ± 1.00
	b 15/20	1.70 ± 1.34		
Chinook	a 6/19	0.68 ± 1.29	a 7/21	0.90 ± 1.18
	b 10/20	1.80 ± 1.86	b 10/20	1.30 ± 1.49
			c 16/43	0.77 ± 1.19
together				
Chum:	a 8/10	1.70 ± 1.06	a 9/10	1.90 ± 0.99
	b 5/9	1.11 ± 1.17	b 8/10	1.40 ± 0.97
	c 2/9	0.33 ± 0.71	c 6/7	1.57 ± 0.97
	d 5/10	0.90 ± 0.99		
Chinook	a 4/11	0.73 ± 1.10	a 7/10	1.60 ± 1.43
	b 3/10	0.80 ± 1.47	b 3/9	0.44 ± 0.73
	c 4/10	0.90 ± 1.45	c 4/8	0.50 ± 0.77
	d 5/10	1.50 ± 1.78		

Table 2. Percentage overlap (Schoener`s index; Schoener 1969) in diet composition; % volume and (% number) of the species used in the tidal channel enclosure experiments. The three-species combination was repeated twice in 1986 and the two-species combination replicated on all days except 10 May in 1989. Letters before the data denote the different replicates. For number of fish in each enclosure see Table 1.

	Chum and Pink		**Chinook and Pink**		**Chum and Chinook**	
1986	Alone	Together	Alone	Together	Alone	Together
25 April	86 (100)	85 (98)				
9-10 May	96 (99)	75 (97)	78 (98)	46 (33)	83 (100)	
3 species		a 75 (97)		72 (91)		66 (63)
9-10 May		b 90 (100)		72 (100)		72 (100)

	Chum and chinook	
1989	Alone	Together
20-22 April	a 62 (84)	a 33 (6)
	b 44 (76)	b 38 (89)
		c 0 (0)
		d 20 (68)
8-10 May	46 (94)	a 40 (61)
		b 45 (66)
		c 10 (1)

Table 3. Average (± SD) number of prey per fish, and statistics for fish species as main effect from a two-way MANOVA, with species and treatment (species alone/together) as main effects on number of prey eaten in enclosure experiment 1989, both factors nested within date. The model showed significant effect of fish species (Wilks' $\lambda_{24,325} = 0.61$, $P<0.001$), but not of treatment (Wilks'$\lambda_{24,325} = 0.77$, $p = 0.19$).

	Chinook	Chum	$F_{3,119}$	P
Insect adults	0.39 ± 0.53	0.07 ± 0.25	4.49	0.005
Insect pupae	0.06 ± 0.33	0.03 ± 0.18	0.54	0.66
Insect larvae	0.30 ± 0.53	0.30 ± 0.63	0.40	0.75
Cyclopoda	0.12 ± 0.60	0.21 ± 0.23	0.95	0.42
Neomysis	0.16 ± 0.37	0.06 ± 0.23	1.52	0.21
Corophium	0.22 ± 0.44	0.18 ± 0.37	3.42	0.020
Anisogamm.	0.06 ± 0.24	0.12 ± 0.44	1.81	0.15
Harpacticoids	6.17 ± 15.12	28.72 ± 0.31	9.25	<0.001

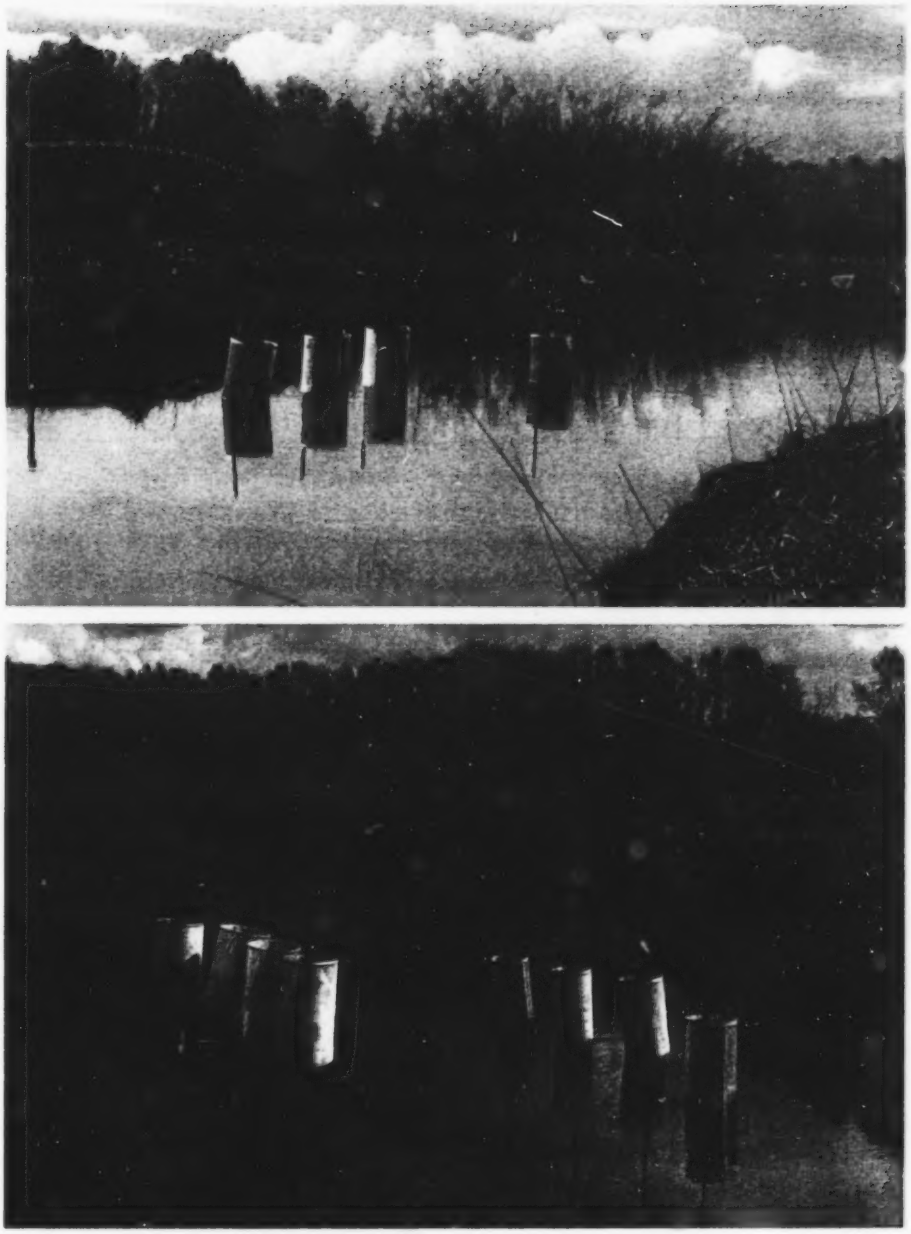

Figure. 1. Enclosures in the Fraser River tidal channel, (above) at intermediate water level and (below) at the end of the experiment with upper halves of the enclosures (on left) removed for easier recapture of salmon fry in lower halves (on right).

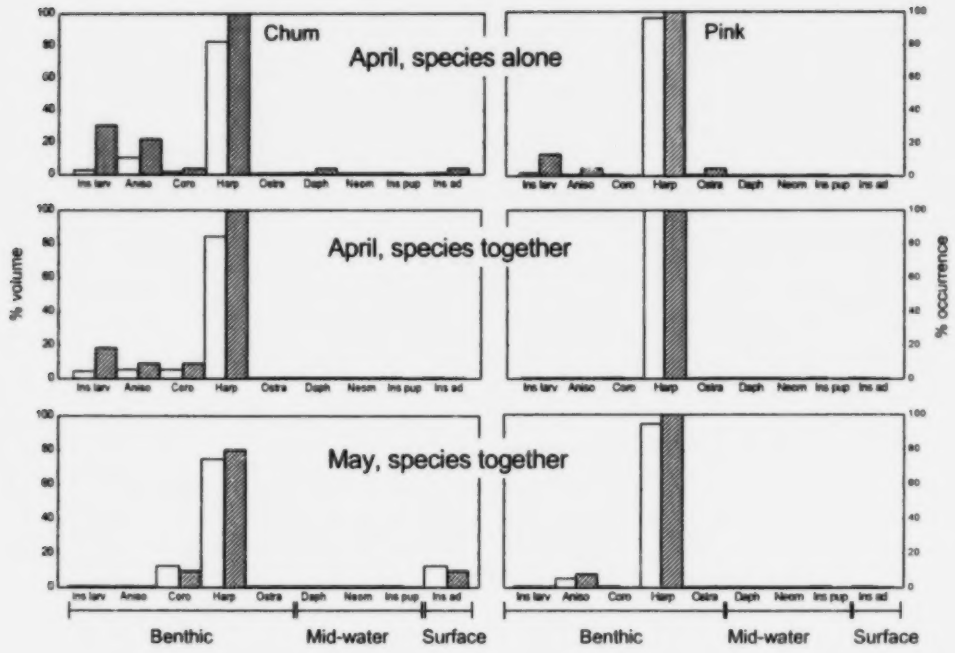

Figure. 2. Contribution of major prey items to food taken by chum and pink fry in enclosure experiments in a Fraser River tidal channel, 25 April (species alone and together in enclosure), and 9 May (species together) 1986. Open bars show % volume and hatched bars % occurrence for the different prey types. Prey are divided into groups with different habitat usage, i.e., benthic, mid-water and surface dwelling species. The prey types are, from left to right: insect larvae, *Anisogammarus confervicolus*, *Corophium spinicorne*, harpacticoids, ostracods, Daphnia, *Neomysis mercedis*, insect pupae, insect adults.

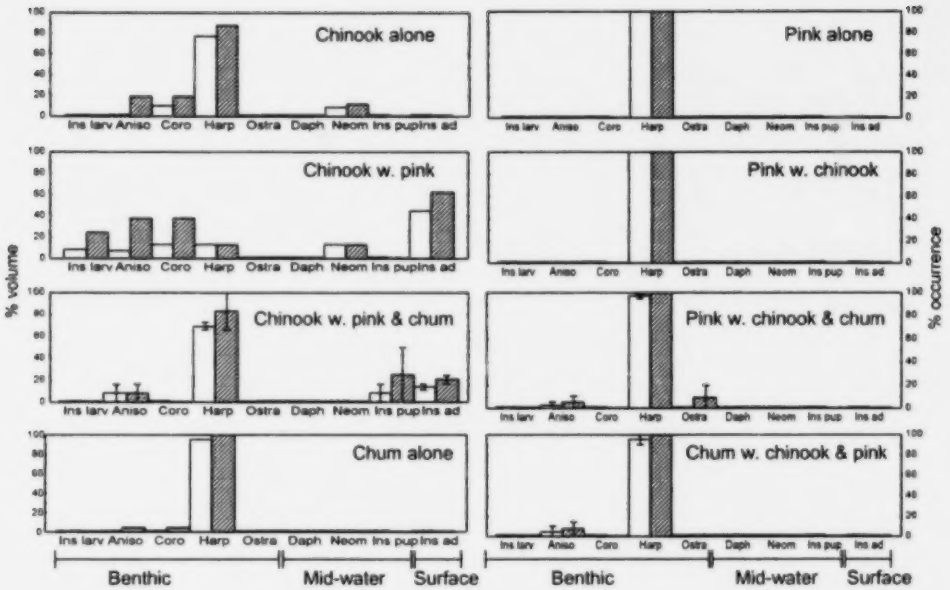

Figure 3. Contribution of major prey items to food taken by chinook, pink and chum fry in enclosure experiments in a Fraser River tidal channel, 9-10 May 1986. Open bars show % volume and hatched bars % occurrence for the different prey types. In the three-species combinations, the mean values of two replicates are shown, and bars show the range. Prey are divided into groups with different habitat usage, i.e. benthic, mid-water and surface dwelling species, for type see Fig. 2.

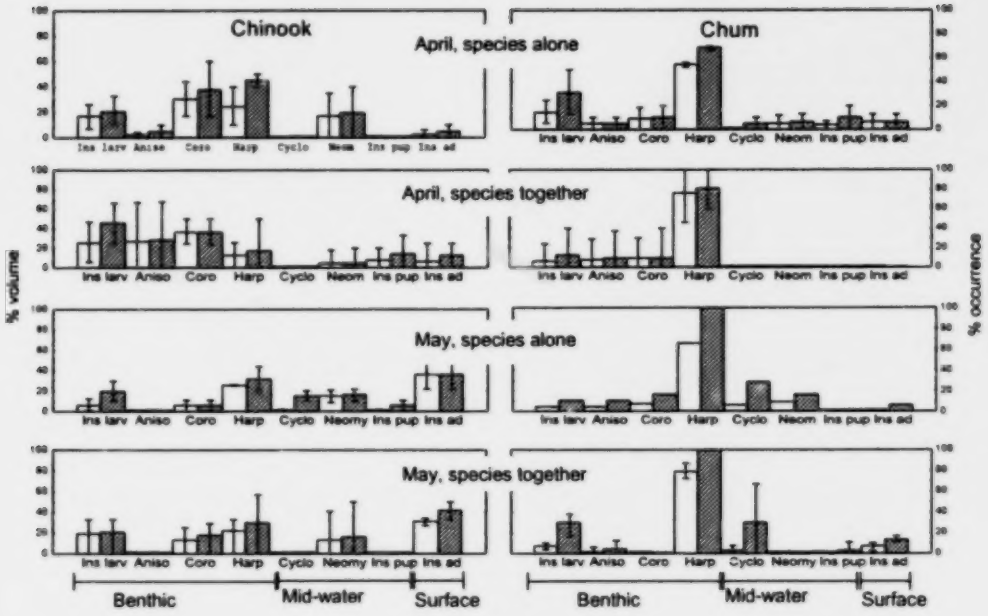

Figure 4. Contribution of major prey items to food taken by chum and chinook fry in enclosure experiments in a Fraser River tidal channel, 1989. Open bars show % volume and hatched bars % occurrence for the different prey types. Diagrams of species alone show the mean value of two replicates; diagrams of species together show means of four (April) or three (May) replicates for each month. Bars show the range of values from enclosures. Prey are divided into groups with different habitat usage, i.e., benthic, mid-water and surface dwelling species. The prey types are, from left to right: insect larvae, *Anisogammarus confervicolus*, *Corophium spinicorne*, harpacticoids, cyclopods, *Neomysis mercedis*, insect pupae, insect adults.

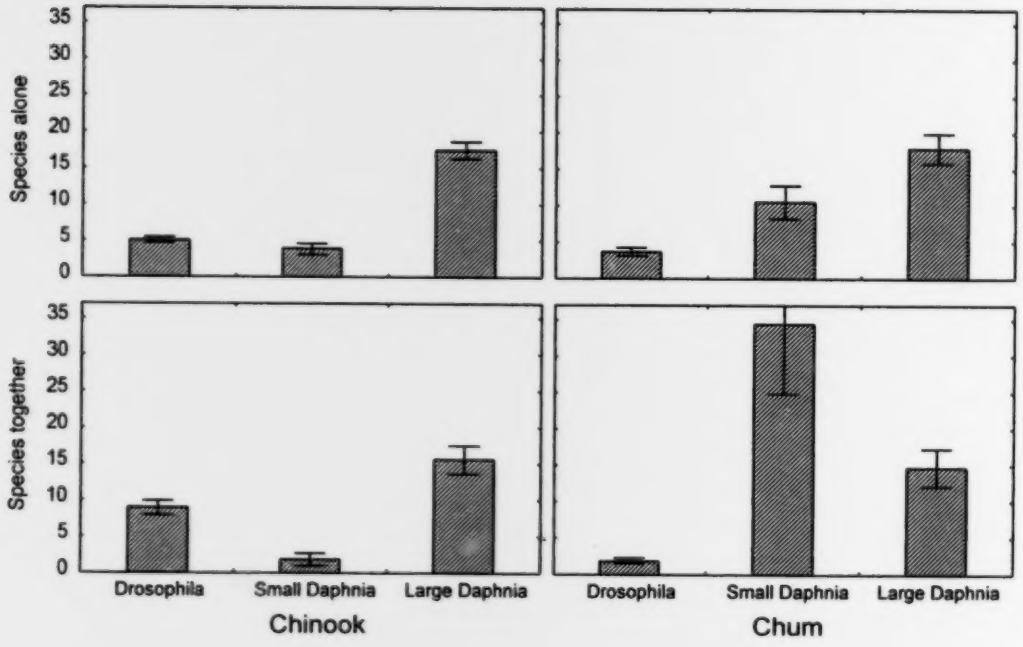

Figure 5. Average number (± SD) of prey taken by chum and chinook when species were held alone (n=8) and together (n=16) in aquarium experiments.

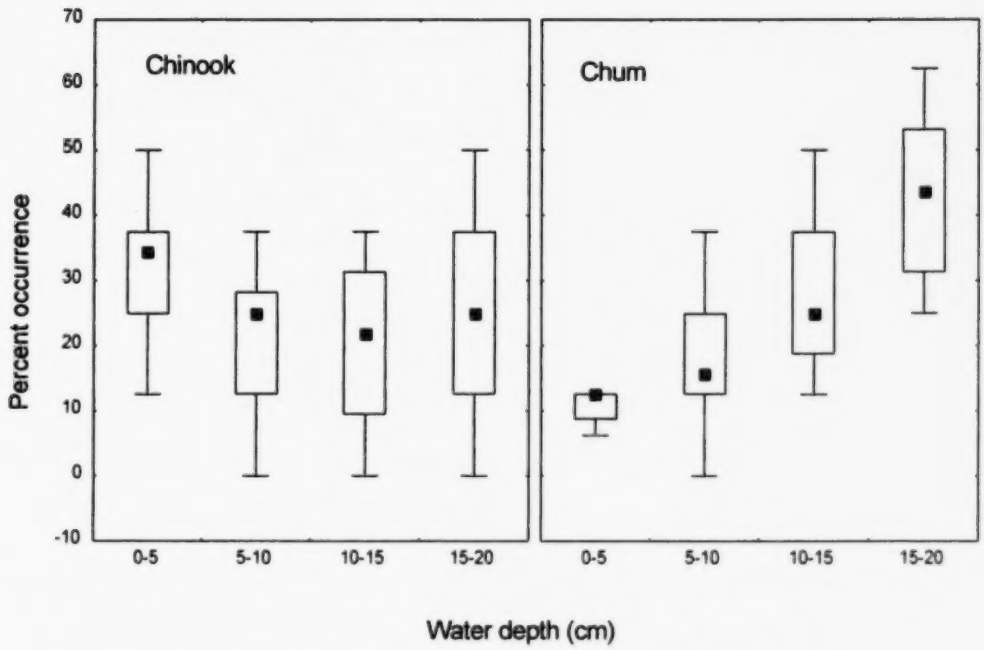

Figure. 6. Depth distribution by chum and chinook in aquarium experiments. Results are pooled for treatments with species alone (n = 4) and together (n = 8), in aquaria with clear water. The boxplots shows median, quartiles, maximum and minimum.